

# Opuntia (Cactaceae; Opuntioideae) Flower-Visiting Insects

Subjects: Biodiversity Conservation | Ecology | Entomology

Contributor: Alfredo Ramírez-Hernández

*Opuntia* species are cacti with high ecological, economic and conservation interest in semiarid environments, particularly in Mexico. Despite the economic and cultural importance of *Opuntia*, there is a significant lack of knowledge about the flower-visiting insects and their taxonomic identity. Although some *Opuntia* species could be visited by birds such as hummingbirds, the most dominant taxonomic group of pollinators are the insects.

Keywords: insecta ; pollination ; drylands ; core species ; conservation

---

## 1. Introduction

Cactaceae Juss, 1789, is a highly diversified family of xerophytes that are dominant through the arid and semiarid environments of the Americas, which is its center of origin and diversification <sup>[1]</sup>. Cacti comprise approximately 1400–1800 described species in the world <sup>[2][3][4]</sup>, and Mexico is the country with the greatest diversity, with 52 genera and 850 species, of which an estimated 84% are endemic <sup>[4][5]</sup>. In addition, nearly 31% of cacti are globally threatened <sup>[6]</sup> due to changes in land use; introduction of exotic species; and uncontrolled harvesting of these plants for use as food, raw material, and other purposes <sup>[7]</sup>. Some of them are listed by the International Union for the Conservation of Nature (IUCN) under various threat categories (<https://www.iucnredlist.org/>, accessed on 22 April 2021), which points to the need for conservation efforts.

*Opuntia* Mill. (Cactaceae; Opuntioideae) is the richest genus within the Cactaceae with nearly 200 described species <sup>[2][8]</sup>. *Opuntia* species are well-adapted to drought-stressed conditions <sup>[10]</sup>, being highly distributed throughout arid and semiarid environments <sup>[9]</sup>. The genus *Opuntia* is endemic to the Americas and it is distributed from Canada to Argentina <sup>[8]</sup>, showing a high number of regional endemic species in Mexico <sup>[11]</sup>.

However, some *Opuntia* species were introduced to other continents after the Spanish conquest <sup>[12][13][14]</sup> due to their traditional uses as medicinal plants, fruits, vegetables, dyes, food ingredients, and forage, among others <sup>[15][16][17][18]</sup>.

In some cases, they have been naturalized <sup>[19][20]</sup>, often resulting in problems for conservation efforts, as in Spain <sup>[20]</sup>. In some other cases, they became naturalized without any ecological problem and became a useful genetic resource with promising potential applications in cosmetics, the pharmaceutical industry, and bioenergy production <sup>[16][17]</sup>. In Mexico, the genus has a marked importance both historically and culturally because of the production of “nopal” (the Mexican denomination for the edible young cladodes developed by cacti species belonging to the genera *Opuntia* and *Nopalea*, which is translated into English as “prickly pear”) and “tuna” (Mexican name for the edible fruit of cacti species belonging to the genera *Opuntia* and *Nopalea*). In this regard, it has been estimated that the exploitation of *Opuntia* plants could generate jobs for approximately 2000 families in rural areas <sup>[21]</sup>.

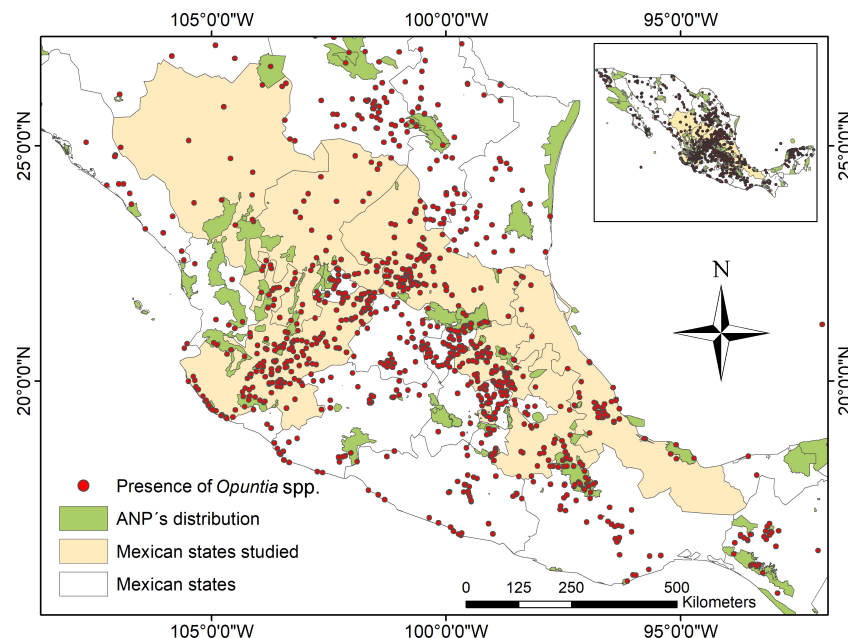
Asexual propagation in *Opuntia* cacti occurs naturally by stem or cladode detachment <sup>[22]</sup>. Nonetheless, sexual reproduction remains important, especially for generating viable genetic pools in wild populations, as well as for the production of “tunas” <sup>[23]</sup>. Sexual reproduction depends mainly on insects <sup>[24][25]</sup>. Therefore, improving our understanding of the relationships between *Opuntia* plants and insect pollination is critical for the conservation of both plants and insects <sup>[26][27][28]</sup> as well as for crop productivity <sup>[24]</sup>.

Insect pollination has probably been crucial for the diversification and success of *Opuntia* in colonizing the American continent <sup>[1][23]</sup>. Bees in particular have been widely recognized as the main pollinators of *Opuntia* species <sup>[29]</sup>, where mellitophilous syndrome dominates <sup>[25]</sup>. Visitation by insects depends on the color and scent of the flower (which is usually hermaphroditic), taste and quality of the nectar, and pollen production <sup>[30]</sup>, as well as on the morphology of the visitors and the spatiotemporal abundance of both flowers and flower visitors <sup>[31]</sup>. Although some *Opuntia* species could be visited by

birds such as hummingbirds (see Pimienta and del Castillo [32]), the most dominant taxonomic group of pollinators are the insects.

## 2. *Opuntia* (Cactaceae; Opuntioideae) Flower-Visiting Insects

In Mexico, *Opuntia* species represent one of the most important crops, because they cover about 30% of the country's land area, and they are mainly distributed throughout arid and semiarid regions (**Figure 1**) [33]. Mexico is the main producer of prickly pears, supporting 43% of annual world production, which is estimated at 1,060,000 t in an area of 100,000 ha [34]. The area planted with "nopal" in Mexico in 2019 was 45,746 ha, which was mainly in the Mexican High Plateau (central Mexico).



**Figure 1.** Distribution of *Opuntia* species throughout Mexico, highlighting the states where studies in articles retrieved were carried out, as extracted from the Global Biodiversity Information (GBIF).

### 2.1. Timeline of *Opuntia* Studies

Since the botanical family Cactaceae is endemic to the Americas [9], it is not surprising to find a higher number of articles published on this continent, particularly in the U.S.A. and Mexico (nine articles each). It is evident that insect pollination attracted the interests of early researchers [35][36], who studied the main flower-visiting insects on *O. humifusa* and *O. macrorhiza*, with a taxonomic description of new bee species of the genus *Perdita* (Hymenoptera) in the U.S.A.

Further research papers were published in the 1970s that were focused on both pollination and the reproductive system of *Opuntia* spp. Grant and Grant [37] and Grant et al. [38] studied the behavior of insects and their efficiency as pollinators of *O. basilaris*, *O. littoralis*, and *O. lindheimeri*. At the end of the 1980s, new research was conducted on flower-visiting insects in San Luis Potosí in the southern Chihuahuan Desert (Mexico) [39][40].

In the twenty-first century, 18 studies have been published around the world: six in Mexico and 12 in other countries. These studies were focused on *Opuntia* biology, including pollinators [41]. Outside of the Americas, *Opuntia* species are recognized as exotic, with some considered fully naturalized, and they are often cultivated and used [42][43]. For example, *Opuntia* species have been exploited since the eighteenth century in Sicily, which is the center of cultivation of this genus in Italy [24]. Other studies addressed the invasive nature of certain *Opuntia* species, which can modify the native community structure due to their greater attraction of native insects in comparison to native plants [19][20][44].

### 2.2. Insect Diversity: Are All the Species Efficient in Pollen Transport?

The studies conducted worldwide indicate that the main flower-visiting insect species in *Opuntia* spp. are bees (Hymenoptera, Apidae), beetles (Coleoptera), and some lepidopterans (Lepidoptera). However, the effectiveness of pollinator species varied broadly. Early studies [37][38] showed that both bees and beetles were the main groups of insects that pollinated *Opuntia* plants; however, beetles species were not found to be efficient for pollen transport because they

feed on the stamens and petals [37][38]. Therefore, the probability of pollen adhering to their bodies is very low [45]. Moreover, beetles do not fly in search of more flowers, and thus, cross-pollination between plants is limited.

In addition, the body size of insects plays a critical role in determining their effectiveness as pollinators [45]. Due to their smaller body size, bees of the genus *Perdita* sp. (2.0 mm to 10.0 mm) are not considered very effective pollinators, because they can slip into a flower without coming into contact with the stigma [38], thus limiting pollination. The recognized effective pollinators of *Opuntia* are medium and large-sized bees, such as species belonging to the genera *Diadasia*, *Lithurge*, *Melissodes*, *Bombus*, *Agapostemon*, and *Megachile* [38][46].

The few studies carried out in Argentina, Brazil and Canada were devoted to learning the structure of *Opuntia* flowers and the diversity of insects that visit them. For example, when bees touch the filaments, they stimulate the movement of sensitive stamens, causing the *Opuntia* flower to hide most of its pollen from flower visitors [23]. This floral adaptation benefits oligolectic (pollen-specialist) pollinating bees, which can reach the lower layers of the anthers, where 80% of the flower pollen is located [47]. According to the results obtained in the meta-analysis, oligolectic species (such as *Ptilothrix fructifera*, *Lithurgus rufiventris* and *Cephalocolletes rugata*) are the only effective pollinators in *Opuntia* [47][48][49]. Reliance on oligolectic bees for pollination has been similarly documented for a high number of plant species belonging to different plant families [50][51], including other Cactaceae [41][52]. Therefore, this seems to be quite likely for all *Opuntia* species as well. However, evidence in studies of other plant taxa highlights that the pollination effectiveness of different flower-visiting insects can also vary depending on other factors, such as season or geographical area, where other insects, including non-oligolectic bees, can act as effective pollinators [50]. For instance, in *Lobularia maritima* (L.) Desv. (Brassicaceae), the effectiveness of ants in pollination during the summer was comparable to the most effective insects in other periods such as spring [50]. Ants were also the main pollinators of *Jatropha curcas* L. (Euphorbiaceae) in Mediterranean croplands, unlike what is described for this species in its native distribution area [53]. As *Opuntia* spp. display a wide blooming period (ranging from early spring to the whole summer), and some of them are important crop species that are commonly grown out of their native area, it would be interesting to examine whether ants (as they are usually documented to be abundant flower visitors) or other animal species might also constitute effective pollinators in certain cases.

However, it is also important to bear in mind that ants (as occurs with other common flower-visiting insects) could not generally participate in active *Opuntia* pollination, as these plants have extrafloral nectaries (EFN). Ecologically, extrafloral nectar is important as a sugared reward for ants to assure ant protection against herbivores [54][55][56]. Having EFN, plants also prevent ants from taking nectar directly from flowers, thus ensuring pollination by other more efficient species [57] in order to achieve successful cross-pollination between different *Opuntia* individuals.

In this regard, ants could be even considered nectar thieves, because the pollen is not transported to other plant individuals as a result of their visit (mainly due to their small body size and absence of hair), and the plant does not benefit from the interaction from the sexual reproduction point of view (e.g., Komamura et al. [58]). Although there are few ant species able to transport pollen, the usual presence of metapleural gland secretion on the integument can also reduce the viability of pollen grains in these particular cases, as documented by Beattie et al. [59], Rostás et al. [60], and Rostás and Tautz [61], therefore, not contributing to the effective cross-pollination. In addition, Rostás et al. [60] found that ants visiting the flowers of *Euphorbia seguieriana* Neck. do not facilitate outcrossing because the worker ants were mainly plant dwellers; therefore, it was only flying insects that were responsible for pollination, thus increasing the real sexual reproduction measured by success in seed germination rates. Therefore, the role of ants (or other animal species) in *Opuntia* pollination beyond oligolectic bees should be carefully studied in order to achieve a better understanding of the reproductive ecology of these plants.

It is well known that cross-pollination mediated by insects in *Opuntia* species is crucial for crop productivity [62]. According to Ávila-Gómez et al. [63], *Opuntia* spp. crop productivity (e.g., number of fruits) is related to the number and species composition of bees. In addition, cross-pollination maintains the genetic diversity in plant populations. Nonetheless, this issue has not been studied for *Opuntia* spp., and further research must focus on understanding how these complex interactions could support the genetic variability of *Opuntia* spp. and the impact it might have on the plant–pollinator network structure.

### 2.3. The Relationship between *Opuntia* and Insects in Mexico

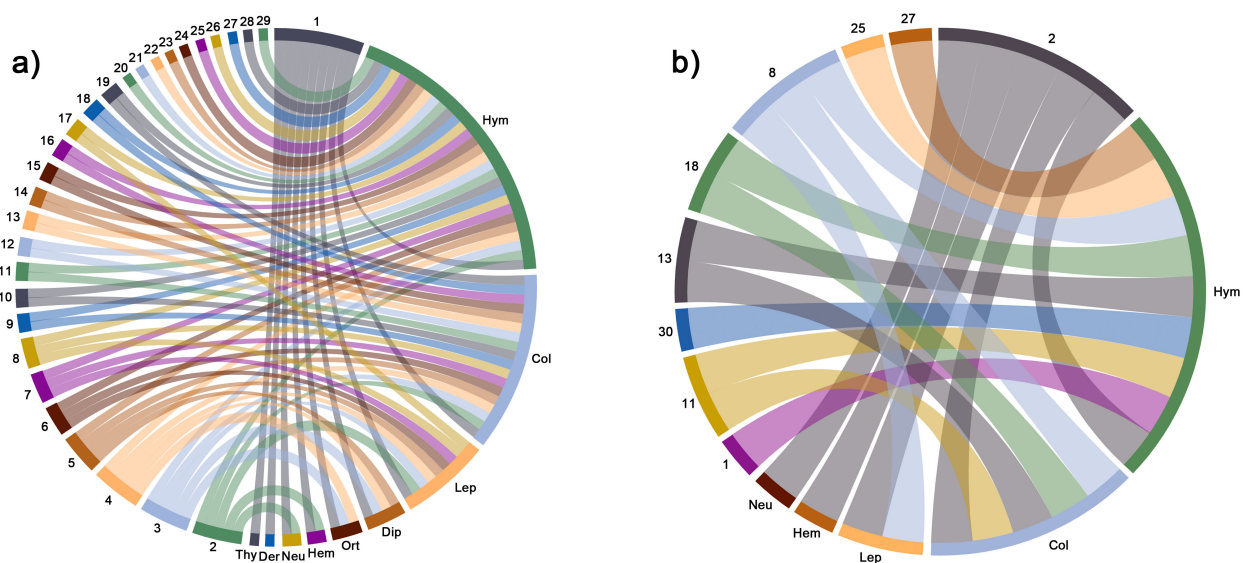
Two studies were conducted in the Mapimi Biosphere Reserve, which is part of the Chihuahuan desert. These studies were focused on *O. rastrera* [40] and *O. microdasys* [64]; however, few records of flower visitors were obtained. In contrast, Morales-Trejo et al. [32] studied the insect diversity associated with *O. pilifera*, and they recorded the highest number of insects so far (Hymenoptera, Coleoptera, Hemiptera, Diptera, Neuroptera, and Lepidoptera were identified). Differences in the number of species recorded could be due to the different sampling methods employed. For instance, studies

performed on *O. rastrera* and *O. microdasys* were focused on visual records of the frequency that insects pollinated *Opuntia* flowers. The research conducted on *O. pilifera* employed a more complete set of harvesting methods mainly consisting of direct collection using entomological nets to capture flying insects and entomological forceps for species found inside the flowers [32]. Santa Anna-Aguayo et al. [65] used a sampling method that consisted of video camera recordings in order to study the behavior of the introduced species *A. mellifera* and the native species *Lithurgus littoralis*. They highlighted possible interference by competition between native and non-native bee species that visit the flowers of *O. huajuapensis*.

The use of diverse sampling methods to study the same group of insects often produces different results. This may generate biased conclusions that in turn make it difficult to compare the diversity of species and interactions, and their implications for biodiversity conservation [66]. It is difficult to standardize a single method for insect sampling, and a recommendation to achieve more complete coverage of diversity is to coordinate all data produced by different sampling approaches [67]. In this regard, assimilating information collected using multiple methods, observations, and other sources into a composite database on *Opuntia* and insect interactions would provide a basis for a better understanding of plant–insect interactions between these groups. Moreover, focusing research efforts on interactions between threatened species of *Opuntia* and insects will help the conservation and management of these species.

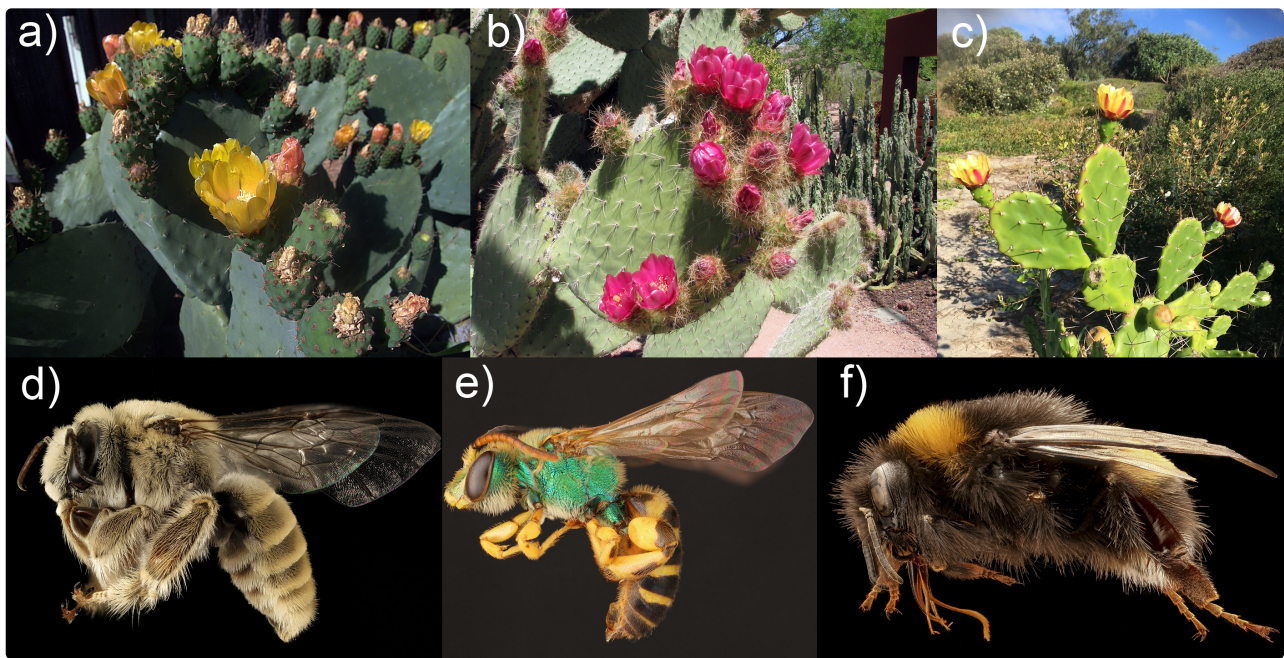
## 2.4. The Role of Core Species in the Community Structure

We found that *O. ficus-indica*, *O. pilifera*, and *O. monacantha* constitute the generalist core of the *Opuntia* spp. global network (Figure 2; 3), whereas only *O. pilifera* was core in the Mexican network (Figure 2). In a broad sense, the importance of *Opuntia* in the network can vary according to the number of studies carried out in each species as well as the sampling effort. This is probably the case for *O. ficus-indica*, which is a domesticated species with a long history of uses and has been cultivated in several countries [68][69].



**Figure 2.** Circular network configuration of flower-visiting orders of insects associated with *Opuntia* species constructed with the databases of the retrieved articles between 1911 and 2020. Databases were sorted to construct a (a) global network and (b) network of Mexico. Numbers and abbreviations are defined as follows: Hym: Hymenoptera; Col: Coleoptera; Lep: Lepidoptera; Dip: Diptera; Ort: Orthoptera; Hem: Hemiptera; Neu: Neuroptera; Der: Dermaptera; Thy: Thysanoptera. 1: *O. ficus-indica*; 2: *O. pilifera*; 3: *O. polyacantha*; 4: *O. fragilis*; 5: *O. stricta*; 6: *O. elata*; 7: *O. maxima*; 8: *O. tomentosa*; 9: *O. monacantha*; 10: *O. lindheimeri*; 11: *O. robusta*; 12: *O. anacantha*; 13: *O. rastrera*; 14: *O. basilaris*; 15: *O. humifusa*; 16: *O. macrorrhiza*; 17: *O. quimilo*; 18: *O. microdasys*; 19: *O. littoralis*; 20: *O. viridirubra*; 21: *O. spinulifera*; 22: *O. sulphurea*; 23: *O. phaeacantha*; 24: *O. retrorsa*; 25: *O. streptacantha*; 26: *O. dillenii*; 27: *O. huajuapensis*; 28: *O. macrocentra*; 29: *O. engelmannii*.





**Figure 2.** Examples of species that constituted part of the core in both global and Mexico networks. Upper figures show the flowering *Opuntia* species **(a)** *O. ficus-indica*, **(b)** *O. pilifera*, and **(c)** *O. monacantha* and lower figures show core bees **(d)** *Diadasia rinconis*, **(e)** *Agapostemon texanus*, and **(f)** *Bombus terrestris*. Note that the photos are not scaled.

For this reason, it is not surprising that *O. ficus-indica* constitutes part of the core species in the global network (**Figure 2a; 3a**). *O. ficus-indica* was first introduced to Europe via Spain during the fifteenth century, and it has been cultivated in many parts of the world for various purposes, including carminic acid extraction from *Dactylopius coccus* Costa, 1835 [48] [70]. In this regard, Padrón et al. [20] found that *O. maxima* is an invader species that behaves as a core species in native communities, where it becomes naturalized. It is known that flowers of alien plants are usually compatible with the body size of native insects [71]. Accordingly, these plants may attract a broad number of native insect pollinators, acting as competitors of the native flora, modifying the network's structure and the function of the original communities because pollen transported by insects may be dominated by pollen from alien plants [43][72]. In addition, some *Opuntia* species have no limits to their pollen production, so they might sustain a vast community of insects, thus increasing seed production. Therefore, the probability that these species would expand their range of distribution is high [19].

In the Mexican network (**Figure 2b**), *O. pilifera* alone constituted the core species. However, these results are probably influenced by the study conducted by Morales-Trejo et al. [32], who carried out extensive field observations with the goal of recording the highest possible number of insect species and individuals visiting the flowers of *O. pilifera* and finding seven orders of insects. They also found a temporal segregation of insects in the morning versus the afternoon. This variation can most likely be attributed to the environmental pulses that occur at different times of the day because of changes in the main abiotic factors across the day (such as humidity, temperature, solar irradiation, etc.), which can affect insect behavior and activity [73]. More comprehensive studies on the pollination ecology of *Opuntia* species from Mexico, ideally conducted with standardized insect harvesting methodologies, would be necessary to ascertain whether *O. pilifera* is still a core species in the Mexican network, as well as to elucidate the role of other *Opuntia* species as core species for this network.

In terms of the insect fauna recorded visiting *Opuntia* flowers, species belonging to the genera *Diadasia*, *Lithurge*, *Melissodes*, *Bombus*, *Agapostemon*, and *Megachile*, which were also the most effective pollinators, were core to the global network. Species of these genera have been documented as the most effective plant pollinators due to their body size [38][46]. The Eurasian honeybee, *A. mellifera*, had the highest core value. Despite the global economic importance of *A. mellifera* [74][75], it is an exotic species in the Americas [76], and its effects on the structure and functioning of native communities should also be considered. In this regard, Santa Anna-Aguayo et al. [65] found that females of *L. littoralis* avoid flowers that have been previously visited by *A. mellifera*. There is still little information about the competition effect of honeybees on native bees, and therefore, general conclusions cannot be stated. In spite of the fact that *A. mellifera* is included in the IUCN Red Lists [77][78], it could be of great interest to assess the effects of this species on the conservation of native pollinators in areas where it is not native, such as the American continent. It is important that future research prioritize the study of native bees to discover their conservation status, since competition with *A. mellifera* could be reducing their populations and affecting the reproductive capacity of *Opuntia* species.

Bumblebees (*Bombus* sp.) face important conservation challenges in North America due to their natural habitat transformation for large-scale intensive agricultural production [79][80][81] with many species included in the IUCN Red Lists. Therefore, to maintain (or recover) the conservation status and population levels of bumblebees, it could be useful to maintain the *Opuntia* species that they visit.

### 3. Conclusions and Future Perspectives

Despite the historical, economical, and cultural importance of *Opuntia* species in Mexico, the scarce number of studies about the insect pollination of these species is remarkable, and research is completely lacking on *Opuntia* with conservation interests. Further research is needed to standardize an effective sampling protocol to monitor the broad insect diversity. Bees have been considered the main and most efficient pollinator insects, and this has probably diverted attention from other entomofauna. More research is needed to improve knowledge of the diversity of flower-visiting insects associated with *Opuntia*, especially directed toward restricted endemic, rare, or threatened plant species. These future studies should analyze the roles of all visitors in natural community maintenance and the influence of crop productivity. In addition, it is important to expand knowledge of both the influence of exotic entomofauna on native fauna, and the impact that exotic *Opuntia* spp. can have on specialized pollinators, thereby providing us with a broader panorama of this interaction. Finally, because pollination is crucial for crop production, a better understanding of ecological interaction networks would inform management measures undertaken to strengthen biodiversity and agriculture sustainability and productivity in arid and marginal lands.

---

### References

1. Hernandez-Hernandez, T.; Brown, J.W.; Schlumpberger, B.O.; Eguiarte, L.E.; Magallón, S. Beyond aridification: Multiple explanations for the elevated diversification of cacti in the new world Succulent Biome. *New Phytol.* 2014, 202, 1382–1397.
2. Anderson, E.F. *The Cactus Family*; Timber Press: Portland, OR, USA, 2001; p. 776.
3. Hunt, D. *The New Cactus Lexicon*; DH Books: Milborne Port, UK, 2006; Volumes 1 and 2, p. 925.
4. Guerrero, P.C.; Majure, L.C.; Cornejo-Romero, A.; Hernández-Hernández, T. Phylogenetic relationships and evolutionary trends in the cactus family. *J. Hered.* 2019, 110, 4–21.
5. González-Medrano, F. *Las Zonas Áridas y Semiáridas de México y su Vegetación*; Instituto Nacional de Ecología–Secretaría del Medio Ambiente y Recursos Naturales: Mexico City, Mexico, 2012; p. 194.
6. Goettsch, B.; Hilton-Taylor, C.; Cruz-Piñón, G.; Duffy, J.P.; Frances, A.; Hernández, H.M.; Inger, R.; Pollock, C.; Schipper, J.; Superina, M.; et al. High proportion of cactus species threatened with extinction. *Nat. Plants* 2015, 1, 1–7.
7. Jiménez-Sierra, C.L. Las cactáceas mexicanas y los riesgos que enfrentan. *Revista Digital Universitaria* 2011, 12, 5–13.
8. Majure, L.C.; Puente, R. Phylogenetic relationships and morphological evolution in *Opuntia* s. str. and closely related members of tribe Opuntieae. *Succ. Plant Res.* 2014, 8, 9–30.
9. Majure, L.C.; Puente, R.; Griffith, M.P.; Judd, W.S.; Soltis, P.S.; Soltis, D.E. Phylogeny of *Opuntia* s.s. (Cactaceae): Clade delineation, geographic origins, and reticulate evolution. *Am. J. Bot.* 2012, 99, 847–864.
10. Aliscioni, N.L.; Delbón, N.E.; Gurrich, D.E. Spine function in Cactaceae, a review. *J. Prof. Assoc. Cactus* 2021, 23, 1–11.
11. González-Elizondo, M.S.; González-Elizondo, M.; López-Enríquez, I.L.; Tena-Flores, J.A.; González-Gallegos, J.G.; Ruacho-González, L.; Melgoza-Castillo, A.; Villarreal-Quintanilla, J.A.; Estrada-Castillón, A.E. Diagnóstico del conocimiento taxonómico y florístico de las plantas vasculares del norte de México. *Bot. Sci.* 2017, 95, 760–779.
12. Flores Valdez, C.A.; Aguirre Rivera, J.R. *El Nopal como Forraje*; Universidad Autónoma Chapingo: Texcoco, México, 1979; p. 91.
13. Anaya-Pérez, M.A.; Bautista-Zane, R. El nopal forrajero en México: Del siglo XVI al siglo XX. *Agric. Soc. Desarro.* 2008, 5, 167–183.
14. Ortega-Baes, P.; Sührling, S.; Sajama, J.; Sotola, E.; Alonso-Pedano, M.; Bravo, S.; Godínez-Alvarez, H. Diversity and conservation in the Cactus family. In *Desert Plants. Biology and Biotechnology*, 1st ed.; Ramawat, K., Ed.; Springer: Berlin/Heidelberg, Germany, 2009; pp. 157–173.

15. Dubeux, J.C.B., Jr.; Dos Santos, M.V.F.; Da Cunha, M.V.; Dos Santos, D.C.; De Almeida Souza, R.T.; De Mello, A.C.L.; De Souza, T.C. Cactus (*Opuntia* and *Nopalea*) nutritive value: A review. *Anim. Feed Sci. and Tech.* 2021, 275, 114890.
16. Ciriminna, R.; Chavarría-Hernández, N.; Rodríguez-Hernández, A.I.; Pagliaro, M. Toward unfolding the bioeconomy of nopal (*Opuntia* spp.). *Biofuel Bioprod. Bior.* 2019, 13, 1417–1427.
17. Le Houerou, H.N. Utilization of fodder trees and shrubs in the arid and semiarid zones of West Asia and North Africa. *Arid Soil Res. Rehabil.* 2000, 14, 101–135.
18. Silva, M.A.; Albuquerque, T.G.; Pereira, P.; Ramalho, R.; Vicente, F.; Oliveira, M.B.P.; Costa, H.S. *Opuntia ficus-indica* (L.) Mill.: A multi-benefit potential to be exploited. *Molecules* 2021, 26, 951.
19. Bartomeus, I.; Vilà, M. Breeding system and pollen limitation in two supergeneralist alien plants invading Mediterranean shrublands. *Aust. J. Bot.* 2009, 57, 109–115.
20. Padrón, B.; Traveset, A.; Biedenweg, T.; Díaz, D.; Nogales, M.; Olesen, J.M. Impact of alien plant invaders on pollination networks in two archipelagos. *PLoS ONE* 2009, 4, e6275.
21. Instituto Nacional de Estadística y Geografía (INEGI). Características Principales del Cultivo del Nopal en el Distrito Federal Caso Milpa Alta; Censo Agropecuario 2007; Instituto Nacional de Estadística y Geografía: Aguascalientes, Mexico, 2007; p. 68.
22. Rebman, J.P.; Pinkava, D.J. *Opuntia* cacti of North America: An overview. *Fla. Entomol.* 2001, 84, 474–483.
23. Reyes-Agüero, J.A.; Valiente-Banuet, A. Reproductive biology of *Opuntia*: A review. *J. Arid Environ.* 2006, 64, 549–585.
24. Inglese, P.; Mondragon, C.; Nefzaoui, A.; Saenz, C.; Taguchi, M.; Makkar, H.; Louhaichi, M. *Ecología del Cultivo, Manejo y Usos del Nopal*; Food and Agriculture Organization of the United Nations (FAO): Rome, Italy, 2018; p. 229. Available online: <https://hdl.handle.net/20.500.11766/9380> (accessed on 22 October 2021).
25. Mandujano, M.C.; Carrillo-Ángeles, I.; Martínez Peralta, C.; Golubov, J. Reproductive biology of Cactaceae. In *Desert Plants. Biology and Biotechnology*, 1st ed.; Ramawat, K., Ed.; Springer: Berlin/Heidelberg, Germany, 2009; pp. 197–230.
26. Kearns, C.A.; Inouye, D.W.; Waser, N.M. Endangered mutualisms: The conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.* 1998, 29, 83–112.
27. Taki, H.; Kevan, P.G. Does habitat loss affect the communities of plants and insects equally in plant–pollinator interactions? Preliminary findings. *Biodivers. Conserv.* 2007, 16, 3147–3161.
28. Senapathi, D.; Biesmeijer, J.C.; Breeze, T.D.; Kleijn, D.; Potts, S.G.; Carvalheiro, L.G. Pollinator conservation—The difference between managing for pollination services and preserving pollinator diversity. *Curr. Opin. Insect Sci.* 2015, 12, 93–101.
29. Potts, S.G.; Biesmeijer, J.C.; Kremen, C.; Neumann, P.; Schweiger, O.; Kunin, W.E. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 2010, 25, 345–353.
30. Van der Kooi, C.J.; Vallejo-Marín, M.; Leonhardt, S.D. Mutualisms and (A) symmetry in plant-pollinator interactions. *Curr. Biol.* 2021, 31, 91–99.
31. Morales-Trejo, J.J.; Sandoval-Ruiz, C.A.; Fascinetto-Zago, P.; Cruzado-Lima, A.L.; Vázquez-Hernández, C. Abundancia y diversidad de visitantes florales de *Opuntia pilifera* en Zapotitlán Salinas, Puebla. *Entomol. Mex.* 2014, 1, 1144–1148.
32. Pimienta, B.E.; Del Castillo, R.F. Reproductive biology. In *Cacti: Biology and Uses*; Nobel, P.S., Ed.; University of California Press: Los Angeles, CA, USA, 2002; pp. 75–90.
33. Gallegos-Vázquez, C.; Méndez-Gallegos, S.D.J.; Mondragón, J.C. Producción Sustentable de Tuna en San Luis Potosí; Colegio de Postgraduados–Fundación Produce San Luis Potosí: San Luis Potosí, Mexico, 2013; p. 203.
34. Potgieter, J.; D’Aquino, S. Fruit production and post-harvest management. In *Ecología del Cultivo, Manejo y Usos del Nopal*; Inglese, P., Mondragon, C., Nefzaoui, A., Saenz, C., Taguchi, M., Makkar, H., Louhaichi, M., Eds.; Food and Agriculture Organization of the United Nations (FAO): Rome, Italy, 2018; pp. 51–71. Available online: <https://hdl.handle.net/20.500.11766/9380> (accessed on 13 December 2021).
35. Bembower, W. Pollination notes from the Cedar Point region. *Ohio Nat.* 1911, 9, 378–383.
36. Cockerell, T.D.A. Two new subgenera of north American bees. *Am. Mus. Novit* 1922, 47, 1–5.
37. Grant, V.; Grant, K.A. Pollination of *Opuntia basilaris* and *O. littoralis*. *Plant Syst. Evol.* 1979, 132, 321–325.
38. Grant, V.; Grant, K.A.; Hurd, P.D. Pollination of *Opuntia lindheimeri* and related species. *Plant Syst. Evol.* 1979, 132, 313–320.

39. Del Castillo, R.; González-Espinosa, M. Una interpretación evolutiva del polimorfismo sexual de *Opuntia robusta* (Cactaceae). *Agrociencia* 1988, 71, 185–196.
40. Mandujano, M.D.C.; Montaña, C.; Eguiarte, L.E. Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert: Why are sexually derived recruitments so rare? *Am. J. Bot.* 1996, 83, 63–70.
41. Fachardo, A.L.S.; Sigrist, M.R. Pre-zygotic reproductive isolation between two synchronopatric *Opuntia* (Cactaceae) species in the Brazilian Chaco. *Plant Biol.* 2020, 22, 487–493.
42. Pretto, F.; Celesti-Gradow, L.; Carli, E.; Blasi, C. Influence of past land use and current human disturbance on non-native plant species on small Italian islands. *Plant Ecol.* 2010, 210, 225–239.
43. Lo Verde, G.; La Mantia, T. The role of native flower visitors in pollinating *Opuntia ficus-indica* (L.) Mill., naturalized in Sicily. *Acta Oecologica* 2011, 37, 413–417.
44. Bartomeus, I.; Vilà, M.; Santamaría, L. Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia* 2008, 155, 761–770.
45. Jauker, F.; Speckmann, M.; Wolters, V. Intra-specific body size determines pollination effectiveness. *Basic Appl. Ecol.* 2016, 17, 714–719.
46. Osborn, M.M.; Kevan, P.G.; Lane, M.A. Pollination biology of *Opuntia polyacantha* and *Opuntia phaeacantha* (Cactaceae) in southern Colorado. *Plant Syst. Evol.* 1988, 159, 85–94.
47. Cota-Sánchez, J.H.; Almeida, O.J.G.; Falconer, D.J.; Choi, H.J.; Bevan, J. Intriguing thigmonastic (sensitive) stamens in the plains prickly pear *Opuntia polyacantha* (Cactaceae). *Flora* 2013, 208, 381–389.
48. Schlindwein, C.; Wittmann, D. Stamen movements in flowers of *Opuntia* (Cactaceae) favour oligolectic pollinators. *Plant Syst. Evol.* 1997, 204, 179–193.
49. Lenzi, M.; Orth, A.I. Floral visitors of the *Opuntia monacantha* (Cactaceae) in sandbank of the Florianópolis, SC, Brazil. *Acta Biológica Paranaense* 2011, 40, 19–32.
50. Gómez, J.M. Effectiveness of ants as pollinators of *Lobularia maritima*: Effects on main sequential fitness components of the host plant. *Oecologia* 2000, 122, 90–97.
51. Maubecin, C.C.; Boero, L.; Sérsic, A.N. Specialisation in pollen collection, pollination interactions and phenotypic variation of the oil-collecting bee *Chalepogenus cocuccii*. *Apidologie* 2020, 51, 710–723.
52. Arroyo-Pérez, E.; Jiménez-Sierra, C.L.; Zavala Hurtado, J.A.; Flores, J. Shared pollinators and sequential flowering phenologies in two sympatric cactus species. *Plant Ecol. Evo.* 2021, 154, 28–38.
53. Samra, S.; Samocha, Y.; Eisikowitch, D.; Vaknin, Y. Can ants equal honeybees as effective pollinators of the energy crop *Jatropha curcas* L. under Mediterranean conditions? *GCB Bioenergy* 2014, 6, 756–767.
54. Pickett, C.H.; Clark, W.D. The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). *Am. J. Bot.* 1979, 66, 618–625.
55. LeVan, K.E.; Hung, K.L.J.; McCann, K.R.; Ludka, J.T.; Holway, D.A. Floral visitation by the Argentine ant reduces pollinator visitation and seed set in the coast barrel cactus, *Ferocactus viridescens*. *Oecologia* 2014, 174, 163–171.
56. Mauseth, J.D.; Rebmann, J.P.; Machado, S.R. Extrafloral nectaries in cacti. *Cactus Succul. J.* 2016, 88, 156–171.
57. Wagner, D.; Kay, A. Do extrafloral nectaries distract ants from visiting flowers? An experimental test of an overlooked hypothesis. *Evol. Ecol. Res.* 2002, 4, 293–305.
58. Komamura, R.; Koyama, K.; Yamauchi, T.; Konno, Y.; Gu, L. Pollination contribution differs among insects visiting *Cardiocrinum cordatum* flowers. *Forests* 2021, 12, 452.
59. Beattie, A.J.; Turnbull, C.; Knox, R.B.; Williams, E.G. Ant inhibition of pollen function—A possible reason why ant pollination is rare. *Am. J. Bot.* 1984, 71, 421–426.
60. Rostás, M.; Bollmann, F.; Saville, D.; Riedel, M. Ants contribute to pollination but not to reproduction in a rare calcareous grassland forb. *PeerJ* 2018, 6, e4369.
61. Rostás, M.; Tautz, J. Ants as pollinators of plants and the role of floral scents. In *All Flesh is Grass. Cellular Origin, Life in Extreme Habitats and Astrobiology*, 1st ed.; Dubinsky, Z., Seckbach, J., Eds.; Springer: Dordrecht, The Netherlands, 2010; Volume 16, pp. 149–161.
62. Gallai, N.; Salles, J.M.; Settele, J.; Vaissière, B.E. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* 2009, 68, 810–821.
63. Ávila-Gómez, E.S.; Meléndez-Ramírez, V.; Castellanos, I.; Zuria, I.; Moreno, C.E. Prickly pear crops as bee diversity reservoirs and the role of bees in *Opuntia* fruit production. *Agric. Ecosyst. Environ.* 2019, 279, 80–88.



64. Piña, H.H.; Montaña, C.; Mandujano, M. Fruit abortion in the Chihuahuan-Desert endemic cactus *Opuntia microdasys*. *Plant Ecol.* 2007, 193, 305–313.
65. Santa Anna-Aguayo, A.I.; Schaffner, C.M.; Golubov, J.; López-Portillo, J.; García-Franco, J.; Herrera-Meza, G.; Martínez, A.J. Behavioral repertoires and interactions between *Apis mellifera* (Hymenoptera: Apidae) and the native bee *Lithurgus littoralis* (Hymenoptera: Megachilidae) in flowers of *Opuntia huajuapensis* (Cactaceae) in the Tehuacan desert. *Fla. Entomol.* 2017, 100, 396–402.
66. McCravy, K.W. A review of sampling and monitoring methods for beneficial arthropods in agroecosystems. *Insects* 2018, 9, 170.
67. Montgomery, G.A.; Belitz, M.W.; Guralnick, R.P.; Tingley, M.W. Standards and best practices for monitoring and benchmarking insects. *Front. Ecol. Evol.* 2021, 8, 579193.
68. Viguera, A.L.; Portillo, L. Uses of *Opuntia* species and the potential impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in Mexico. *Fla. Entomol.* 2001, 84, 493–498.
69. Griffith, M.P. The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): New molecular evidence. *Am. J. Bot.* 2004, 91, 1915–1921.
70. Barbera, G.; Carimi, F.; Inglese, P. Past and present role of the indian-fig prickly-pear (*Opuntia ficus-indica* (L.) Miller, Cactaceae) in the agriculture of Sicily. *Econ. Bot.* 1992, 46, 10–20.
71. Stang, M.; Klinkhamer, P.G.; Van Der Meijden, E. Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos* 2006, 112, 111–121.
72. Lopezaraiza-Mikel, M.E.; Hayes, R.B.; Whalley, M.R.; Memmott, J. The impact of an alien plant on a native plant–pollinator network: An experimental approach. *Ecol. Lett.* 2007, 10, 539–550.
73. Ness, J.H. Hot spots and hot moments for on-plant foraging by ants within the flora of warm North American Deserts. *Am. Midl. Nat.* 2020, 183, 145–163.
74. Vithanage, V. The role of the European honeybee (*Apis mellifera* L.) in avocado pollination. *J. Hortic. Sci.* 1990, 65, 81–86.
75. Rizzardo, R.A.; Milfont, M.O.; Silva, E.; Freitas, B.M. *Apis mellifera* pollination improves agronomic productivity of anemophilous castor bean (*Ricinus communis*). *Anais da Academia Brasileira de Ciências* 2012, 84, 1137–1145.
76. Moritz, R.F.; Härtel, S.; Neumann, P. Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience* 2005, 12, 289–301.
77. De la Rúa, P.; Paxton, R.J.; Moritz, R.F.A.; Roberts, S.; Allen, D.J.; Pinto, M.A.; Cauia, E.; Fontana, P.; Kryger, P.; Bouga, M.; et al. *Apis mellifera*. The IUCN Red List of Threatened Species 2014, e.T42463639A42463665. Available online: [https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European\\_bees.pdf](https://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European_bees.pdf) (accessed on 13 March 2021).
78. Paudel, Y.P.; Mackereth, R.; Hanley, R.; Qin, W. Honeybees (*Apis mellifera* L.) and pollination issues: Current status, impacts, and potential drivers of decline. *J. Agric. Sci.* 2015, 7, 93–109.
79. Gixti, J.C.; Wong, L.T.; Cameron, S.A.; Favret, C. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol. Conserv.* 2009, 142, 75–84.
80. Jacobson, M.M.; Tucker, E.M.; Mathiasson, M.E.; Rehan, S.M. Decline of bumble bees in northeastern North America, with special focus on *Bombus terricola*. *Biol. Conserv.* 2018, 217, 437–445.
81. Hatfield, R.; Jepsen, S.; Thorp, R.; Richardson, L.; Colla, S.; Foltz Jordan, S. *Bombus pensylvanicus*. The IUCN Red List of Threatened Species 2015, e.T21215172A21215281. Available online: <https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T21215172A21215281.en> (accessed on 25 February 2021).